Cytological Aspects of the Mycobiont–Phycobiont Relationship in Lichens

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CYTOLOGICAL ASPECTS OF THE MYCOBIONT–PHYCOBIONT RELATIONSHIP IN LICHENS

Haustorial types, phycobiont cell wall types, and the ultrastructure of the cell surface layers in some cultured and symbiotic myco- and phycobionts*

Rosmarie HONEGGER‡

Abstract: Cytological aspects of the mycobiont–phycobiont contact were investigated in the lichen species *Peltigera aphthosa*, *Cladonia macrophylla*, *Cladonia caespiticia* and *Parmelia tiliacea* by means of freeze-etch and thin sectioning techniques, and by replication of isolated fragments of myco- and phycobiont cell walls.

In the symbiotic state of the mycobionts investigated a thin outermost wall layer with a distinct pattern was observed mainly in the hyphae contacting phycobiont cells and in the upper medullary layer. No comparable structures were noted on the hyphal surface of the cultured mycobionts of the *Cladonia* and *Parmelia* species investigated. A distinct rodlet layer was found on the hyphal surface of the mycobiont of *Peltigera aphthosa*, while mycobionts of *Cladonia macrophylla*, *C. caespiticia* and *Parmelia tiliacea* had a mosaic of small, irregular ridges, each corresponding in its size to a bundle of rodlets on the outermost wall layer. Comparable surface layers have been described in aerial hyphae of a great number of non-lichenized fungi.

The rodlet layer of the mycobiont wall surface of *Peltigera aphthosa* adheres tightly to the outermost layer of the sporopollenin-containing cell wall of the *Coccomyxa* phycobiont. Mature trebouxioid phycobiont cells of the *Cladonia* and *Parmelia* species investigated in the symbiotic state had an outermost wall layer which was structurally indistinguishable from the tessellated surface layer of the mycobiont cells. A rodlet pattern was detected in the outermost wall layer of *Trebouxia* autospores still surrounded by the cellulosic mother cell wall. In mature *Trebouxia* cells the bundles of rodlets became increasingly covered by a homogeneous material, and thus attained the same tessellated pattern which was observed on the mycobiont wall surface. No comparable structures were found on the wall surface after culturing the *Trebouxia* phycobionts axenically in liquid media. Confluence of the tessellated surface layers of fungal and algal origin was noted at the contact sites of growing hyphal tips and young *Trebouxia* cells.

The possible correlations between these cytological features and published immunological data on the cell surface of cultured and symbiotic lichen myco- and phycobionts are discussed.

Morphology of different types of mycobiont–phycobiont interactions

The light and electron microscopical data on the mycobiont–phycobiont relationship in naturally grown lichens may be summarized as follows: intracellular haustoria with or without wall appositions (Fig. 1A–B, 2) occur in live phycobiont cells of a great number of rather simple crustose lichens (e.g. Tschermak 1941,

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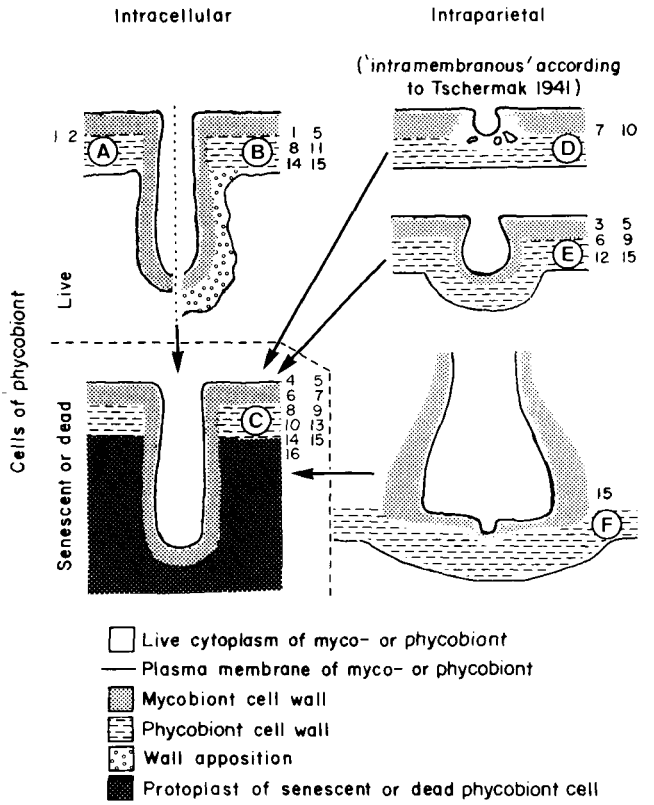


FIG. 1. Diagram of haustorial types so far detected in lichens. The list of references is incomplete, examples only being cited: 1. Ahmadjian (1982), 2, Chapman (1976), 3, Chervin *et al.* (1968), 4, Galun *et al.* (1970*a*), 5, Galun *et al.* (1970*b*), 6, Galun *et al.* (1970*c*), 7, Galun *et al.* (1971*a*), 8, Galun *et al.* (1971*b*), 9, Galun *et al.* (1971*c*), 10, Galun *et al.* (1973), 11, Geitler (1963), 12, Jacobs & Ahmadjian (1971), 13, Peveling (1968), 14, Plessl (1963), 15, Tschermak (1941), 16, Webber & Webber (1970).

Tschermak-Woess 1951, Geitler 1963, Plessl 1963, Peveling 1968, Galun *et al.* 1970*b*, *c*, 1971*b*, Chapman 1976). These intracellular haustoria of lichens are comparable with interface types 18 and 21 of fungal plant pathogens and their hosts as described by Bracker & Littlefield (1973). Intraparietal haustoria (originally described as intramembranous haustoria by Tschermak 1941) which are invading, but not piercing the cell wall of the live phycobiont (Fig. 1D–F, 3, 4) were found in more complex foliose and fruticose groups of lichens (e.g. Tschermak 1941, Plessl 1963, Galun *et al.* 1970*a*, *b*, *c*, 1971*a*, *c*, 1973, Jacobs & Ahmadjian 1971). These intraparietal haustoria may be compared to interface types 34 (Fig. 1D) or 8 respectively (Fig. 1E–F) according to Bracker & Littlefield (1973). In senescent or dead phycobionts of all evolutionary stages, however, intracellular haustoria were detected (e.g. Tschermak 1941, Plessl 1963, Chervin *et al.* 1968, Galun *et al.* 1970*a*, *b*, *c*, 1971*a*, *b*, *c*, 1973, Webber & Webber 1970). This situation is comparable with interface type 19 according to Bracker

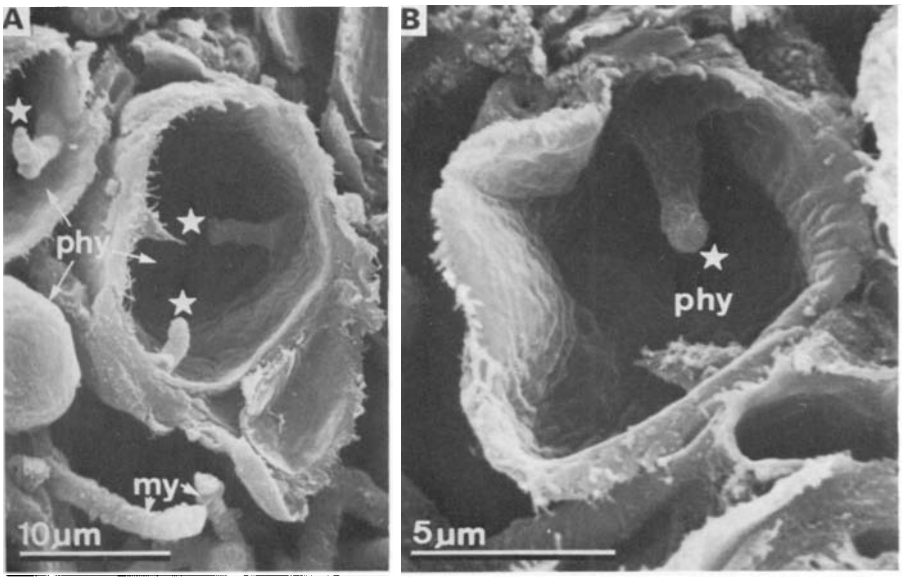


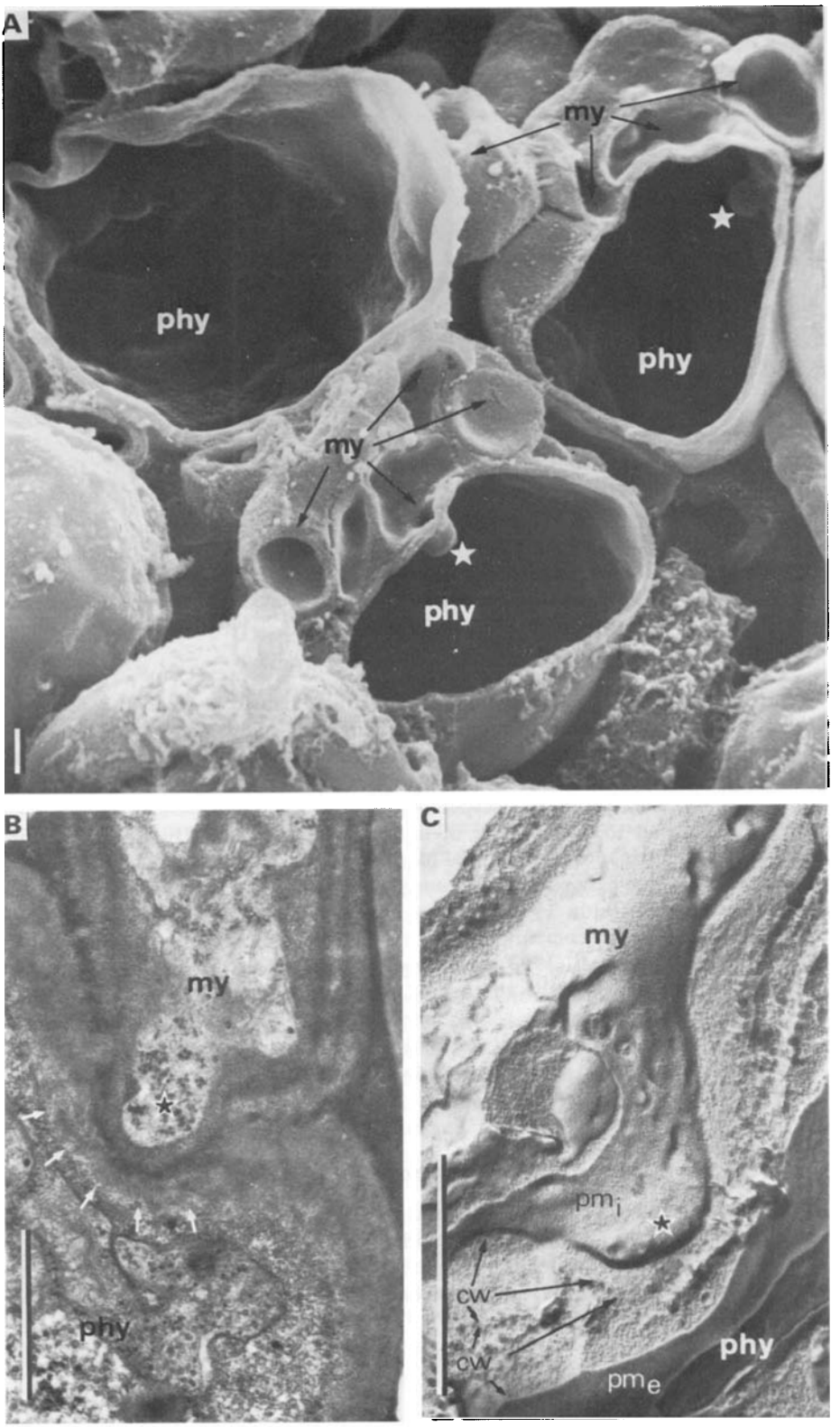
FIG. 2. SEM preparations of intracellular haustoria (*) in sectioned cells of the *Trentepohlia* phycobiont (phy) of *Lecanactis abietina*. my, mycobiont. A, ×2200; B, ×5400.

& Littlefield (1973). Very prominent intracellular haustoria were also detected in axenically resynthesized lichens (Ahmadjian *et al.* 1980, Ahmadjian 1982). In these systems the relationship between myco- and phycobiont seems to be not as delicately balanced as in the naturally grown thalli, or the parasitic character of the mycobiont more prominent respectively.

Very close wall to wall contact of myco- and phycobiont (Fig. 5D, 6A) but neither intracellular, nor intraparietal haustoria were observed in distantly related crustose and foliose lichens with *Coccomyxa* phycobionts (Tschermak 1941, Plessl 1963, Peveling & Galun 1976, Honegger & Brunner 1981, Honegger 1982*a*). This situation is again comparable with interface type 8 according to Bracker & Littlefield (1973). Plessl (1963) presumed the very small size of the phycobiont cells to be the reason for the absence of haustoria. Honegger & Brunner (1981) detected a sporopollenin-like component in the cell wall of various *Coccomyxa* phycobionts and postulated a correlation between the type of mycobiont–phycobiont interaction and the cell wall structure and composition of the phycobiont.

Cell wall structure and composition of lichen phycobionts

Our knowledge of cell wall structure and composition in the taxonomically highly heterogenous group of lichen phycobionts is extremely limited. Ultrastructural studies refer to a noteworthy variation in phycobiont cell wall types (e.g. Peveling 1974, Peveling & Galun 1976, Honegger & Brunner 1981, Honegger 1982*a*, *b*, Withrow & Ahmadjian 1983).



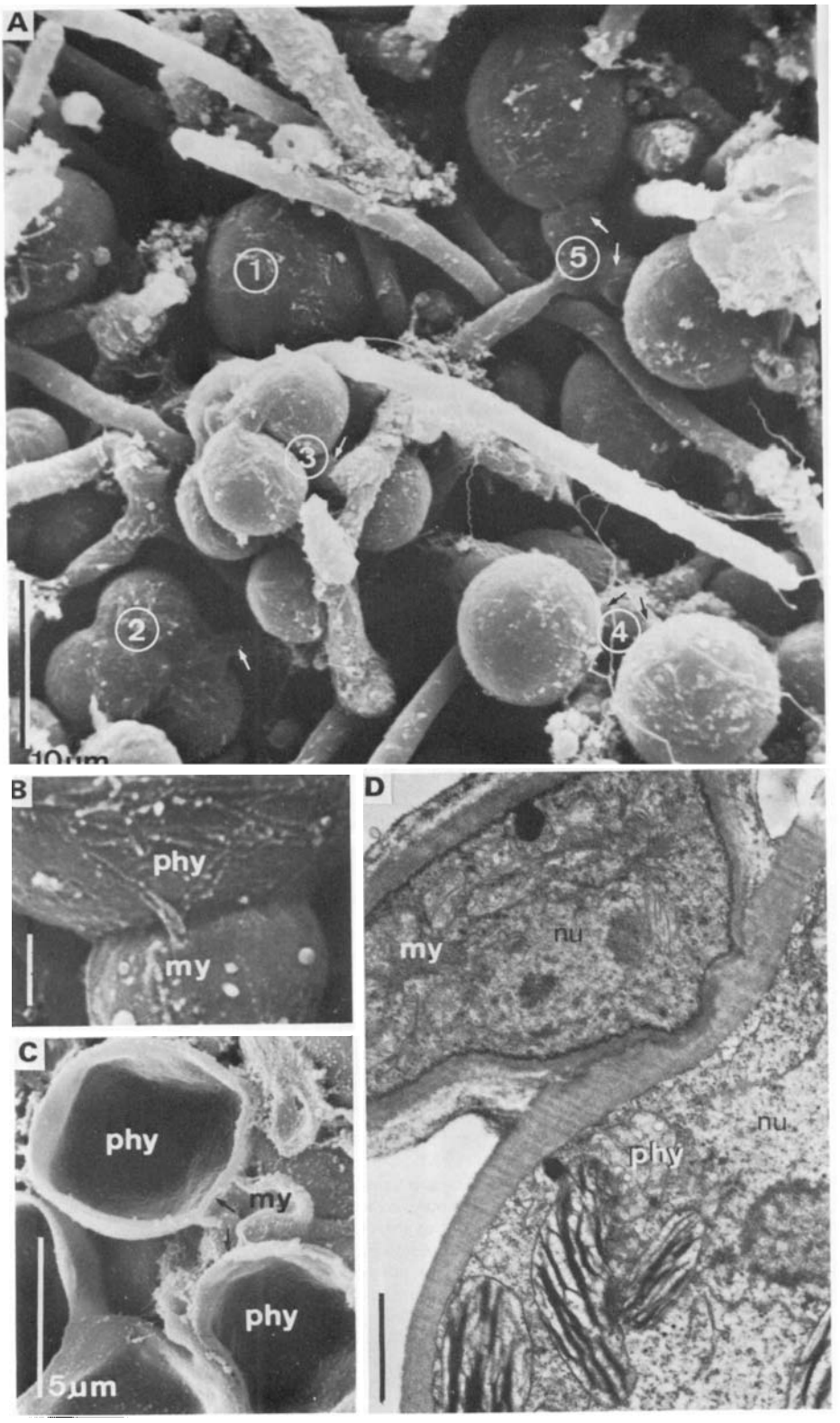
A particularly interesting type of cell wall was found in several *Coccomyxa* and one *Myrmecia* phycobiont of different, distantly related asco- and basidiolichens (Honegger & Brunner 1981). Tripartite cell walls containing an amorphous innermost layer, a thin outer layer with a fibrous, probably cellulosic component, and an outermost trilaminar layer of membrane-like appearance were observed. This trilaminar outermost wall layer contains an acetolysis-resistant, sporopollenin-like component which is not degraded in the lichen thallus (Fig. 5A). Consequently the absence of haustoria in *Coccomyxa* phycobionts was tentatively explained by the problems related to the enzymatical degradation of the very stable biopolymer sporopollenin.

However, it became evident that acetolysis and subsequent infrared spectrophotometry of the residue is not a chemically appropriate method for the characterization of persistant algal cell wall biopolymers as contaminating cellular components such as carotenoids may be condensed during acetolysis and yield acetolysis-resistant residues whose infra-red (IR) spectra closely resemble the spectra of sporopollenin in the range above 1000 cm^{-1} (Berkaloff *et al.* 1983, Brunner, unpublished). With improved methods such as vigorous extraction, saponification and treatment with phosphoric acid (Berkaloff *et al.* 1983) followed by IR spectrophotometry of the residues the presence of a non-degradable, sporopollenin-like component in the cell walls of *Coccomyxa* phycobionts was confirmed, but no persistant cell wall material was found in either *Myrmecia*, *Trebouxia* or *Trentepohlia* phycobionts (Brunner, unpublished). The chemical composition of the trilaminar outermost wall layer of *Myrmecia* phycobionts requires further investigations. It is interesting to note that some *Myrmecia* phycobionts are severely penetrated by intracellular mycobiont haustoria (Tschermak-Woess 1951, Geitler 1963, Ahmadjian 1967, Kilias 1981), while others are not (Honegger & Brunner 1981, Kilias 1981).

A different type of cell wall was observed in phycobionts of the genus *Trebouxia* s.l.* Two wall layers were distinguished in trebouxioid phycobionts with cytochemical (Bubrick & Galun 1980*a*) and cytological methods (Honegger 1982*b*). A relatively thin outer wall layer was stained by Coomassie blue and ruthenium red (Bubrick & Galun, 1980*a*) and thus might contain proteinaceous components and acid polysaccharides. Protein-like particles embedded in an amorphous matrix

*The problems related to the splitting of the chlorophycean genus *Trebouxia* into *Trebouxia* de Puymaly (Chlorococcales) and *Pseudotrebouxia* Archibald (Chlorosarcinales) as proposed by Archibald (1975), Bold & Wynne (1978), and Hildreth & Ahmadjian (1981) are discussed by Tschermak-Woess (1982). Ultrastructural studies are needed.

FIG. 3. SEM and TEM preparations of intraparietal haustoria in living cells of the *Trebouxia* phycobiont of *Cladonia macrophylla*. A, SEM of partly sectioned myco (my)- and phycobiont (phy) cells. An intraparietal haustorium (*) is seen in two out of the three sectioned phycobiont cells. ×6550. B, TEM of an ultrathin section of an intraparietal haustorium (*) at the mycobiont (my)– phycobiont (phy) interface. The cell wall of the phycobiont is not perforated but invaginates around the fungal haustorium (arrows). ×25 000. C, Freeze-fracture preparation of an intraparietal haustorium (*) at the mycobiont (my)– phycobiont (phy) interface. The fracture plane is running along the external face of the phycobiont plasma membrane (pm_e), over the broken cell walls (cw) of phyco- and mycobiont, and along the internal face of the mycobiont plasma membrane (pm_i). ×35 700.



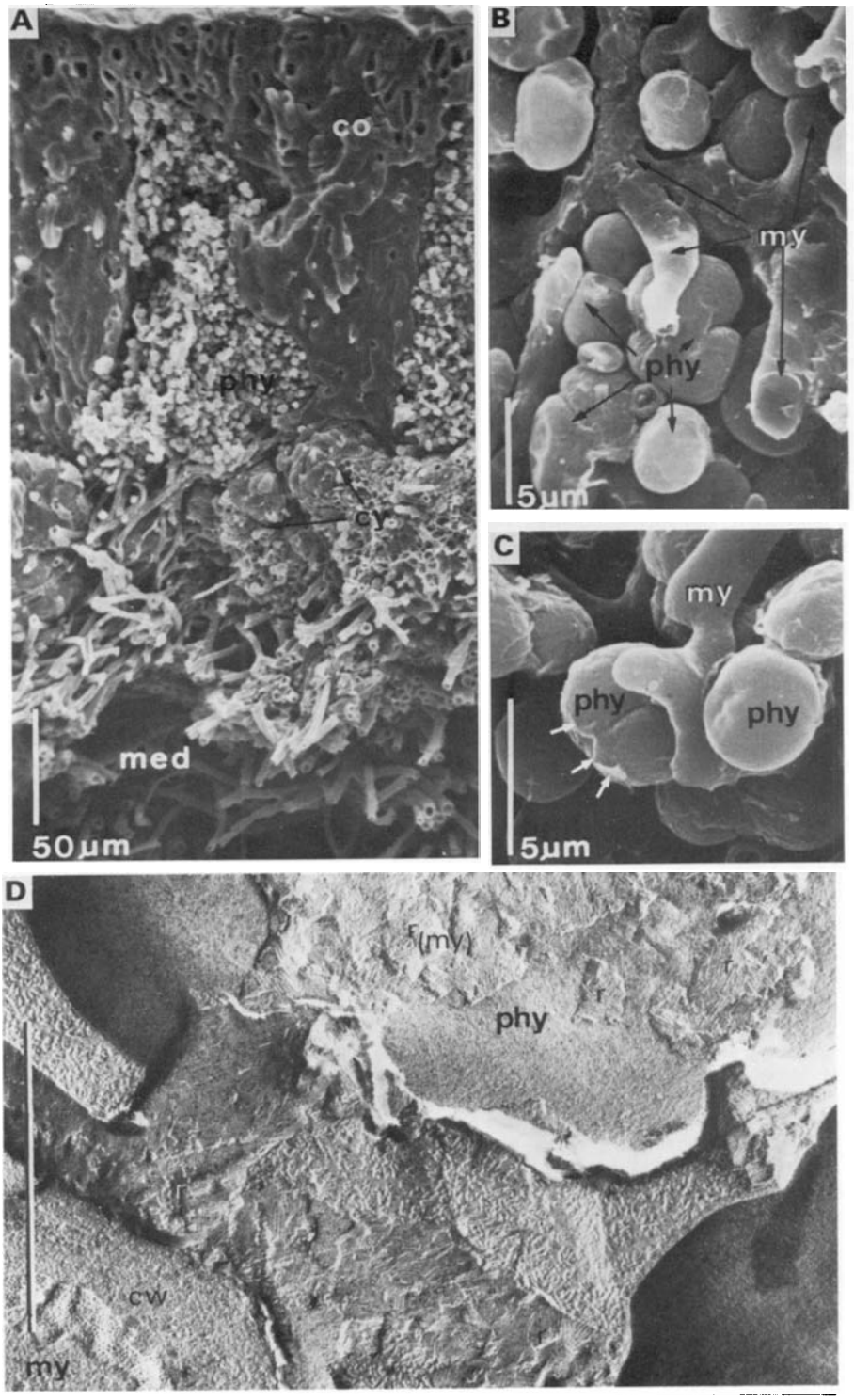
were seen in the outer cell wall layer of cultured *Trebouxia* isolates (Figs 7A, C, 8D; Honegger 1982*b*). The binding of gold-labelled concanavalin A to these protein-like particles was demonstrated with deep-etch techniques (Robenek *et al.* 1982). An inner, more prominent cell wall layer contains a fibrous component embedded in an amorphous matrix (Figs 7B, D, F; Honegger 1982*b*). It has a strong autofluorescence, was stained by chlor-zinc iodine (Tschermak 1941, Plessl 1963, Honegger 1982*b*) and by PAS (Bubrick & Galun 1980*a*). The fluorescence and staining properties indicate polysaccharides, some of which are probably cellulosic.

In contrast to the cell walls of *Coccomyxa* species no non-degradable, persistent parts were detected in the walls of trebouxioid phycobionts (Honegger 1982*b*). The mother cell wall totally disintegrates after autospore formation (Fig. 4A). The amorphous outer wall layer is dissolved and disappears first at the onset of mother cell wall degradation (Figs 7C, E) whereas the inner part of the cell wall attains a burled texture (Figs 7D, F, G) and is degraded somewhat more slowly (Fig. 7F; Honegger 1982*b*). Neither with cytological, nor with chemical methods was a persistant, sporopollenin-like component detected in trebouxioid phycobionts as reported by König & Peveling (1980) on the basis of IR spectrophotometry of acetolysis resistant material. A small, persistant residue whose IR spectra may resemble the spectra of sporopollenin in the range above 1000 cm^{-1}, but not below may be obtained after acetolyzing isolated, purified cell walls of trebouxioid phycobionts, but no residue was detected after vigorous extraction, saponification and phosphoric acid treatment by the method of Berkaloff *et al.* (1983, Brunner, unpublished).

The cell walls of trebouxioid phycobionts may be penetrated by mycobiont haustoria (e.g. Tschermak 1941, Plessl 1963, Durrell 1967, Chervin *et al.* 1968, Peveling 1968, Galun *et al.* 1970*a*, *b*, *c*, 1971*b*, *c*, Webber & Webber 1970, Jacobs & Ahmadjian 1971, Ahmadjian 1982).

Further cytological and chemical studies on cell wall structure and composition in lichen phycobionts are needed to improve our understanding of the symbiotic relationship in lichens.

FIG. 4. SEM and TEM preparations of intraparietal haustoria in members of the Parmeliaceae. A, SEM of external morphology of haustorium formation in *Cetrelia olivetorum*. 1, Large, mature cell of the trebouxioid phycobiont prior to autospore formation; 2, Shortly after autospore formation at the onset of mother cell wall degradation. The arrow points on a growing mycobiont hypha which penetrates the degrading mother cell wall in order to contact the autospores of the phycobiont; 3, Later stage of mother cell wall degradation. The four autospores and a contacting mycobiont hypha (arrow) are well visible; 4, two of four (or more) former autospores of the same mother cell after dissolution of the mother cell wall and increase in size. The contacting mycobiont hypha is branched (arrows); 5, Final stage of haustorial development. Two mature phycobiont cells, both deriving from the same mother cell, and the contacting, branched mycobiont hypha with enlarged, appressoria-like intraparietal haustoria at the contact site with the phycobiont cell (arrows). ×2400. B, Detail of A5: external morphology of a fully developed intraparietal haustorium. ×10 000. C, SEM of sectioned trebouxioid phycobionts (phy) with intraparietal haustoria (arrows) of the mycobiont (my) in *Cetraria islandica*. ×4700. D, Ultrathin section of the mycobiont (my)–phycobiont (phy) interface in a fully developed intraparietal haustorium of *Parmelia tiliacea*. The algal cell wall is thickened at the contact site, but fungal cell wall appears very thin. Nuclei (nu) of both symbionts are seen in the vicinity of the intraparietal haustorium. ×16 500.



Fine structure of the mycobiont–phycobiont interface

Peltigeralean species with Coccomyxa phycobionts

In freeze-fracture studies of *Peltigera aphthosa* (Honegger 1982*a*), *P. venosa* (Fig. 5D), and *Solorina saccata* (unpublished), highly interesting structures were observed at the mycobiont–phycobiont interface. Probably due to their persistent outermost layer with enzymatically non-degradable sporopollenin the cell walls of the *Coccomyxa* phycobionts of the peltigeralean species investigated are not penetrated by mycobiont haustoria. The hyphae of the mycobiont in the algal and upper medullary layer have a thin, semicrystalline outermost wall layer with a distinct rodlet pattern which adheres tightly to the cell wall surface of the *Coccomyxa* phycobiont (Honegger 1982*a*; Fig. 5D). This outermost rodlet layer was not found on the surface of mycobiont hyphae which were either growing within the gelatinous sheath of the colonies of the *Nostoc* cyanobiont, or forming the cortical or lower medullary layer (Honegger 1982*a*). It was not possible to isolate and characterize this rodlet layer, nor could the question be answered whether this structure is a particularity of the symbiotic state or occurs in aerial hyphae of the cultured state as well since these peltigeralean mycobionts could so far not be grown axenically. Structurally very similar rodlet layers have been found on the surface of different types of aerial hyphae in non-lichenized fungi such as vegetative hyphae (Wessels *et al.* 1972) and the hymenial surface of basidiomycetes (Nakai & Ushiyama 1974, McLaughlin 1977, 1982) or conidia and conidiophores of Hyphomycetes (Cole 1973, Hashimoto *et al.* 1976, Beever & Dempsey 1978, Dempsey & Beever 1979, Cole *et al.* 1979, Cole & Pope 1981). The rodlet layers of taxonomically different groups of non-lichenized fungi are chemically surprisingly heterogenous. Proteins, carbohydrates and lipids in varying percentages were detected (Wessels *et al.* 1972, Hashimoto *et al.* 1976, Beever *et al.* 1979, Cole *et al.* 1979, Cole & Pope 1981).

Cladonia and Parmelia species with trebouxioid phycobionts

In light and electron microscopic studies on the mycobiont–phycobiont contact site in structurally complex foliose lichens with trebouxioid phycobionts it became evident that growing mycobiont hyphae contact the algal autospores at a very early

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FIG. 5. SEM and TEM preparations of the mycobiont–phycobiont interface in members of the Peltigerales with *Coccomyxa* species as primary phycobiont and neither intraparietal, nor intracellular haustorium formation but very tight adhesion of the mycobiont hyphae to the sporopollenin-containing outermost cell wall layer of the phycobiont. A–D. SEM and TEM preparations of *Solorina crocea*. A, Cross-section of the thallus, co, cortical zone; phy, phycobiont zone; cy, internal cephalodium containing colonies of the *Nostoc* cyanobiont; med, medullary layer. ×300. B–C. Details of the mycobiont (my)–phycobiont (phy) contact. Arrows point on a thin, but persistent mother cell wall of the very small phycobiont cells. B, ×2000; C, ×4400. D, Freeze-fracture preparation of the mycobiont (my)–phycobiont (phy) contact site in *Peltigera venosa*. The fracture plane follows the broken mycobiont (my) cell, its cell wall (cw) and the inner surface of the outermost cell wall layer; with a distinct rodlet (r) pattern, then the outer surface of the trilaminar, sporopollenin containing outermost cell wall layer of the *Coccomyxa* phycobiont (phy). The outermost wall layer (rodlet layer) of the mycobiont tightly adheres to the phycobiont wall surface. ×42 000.

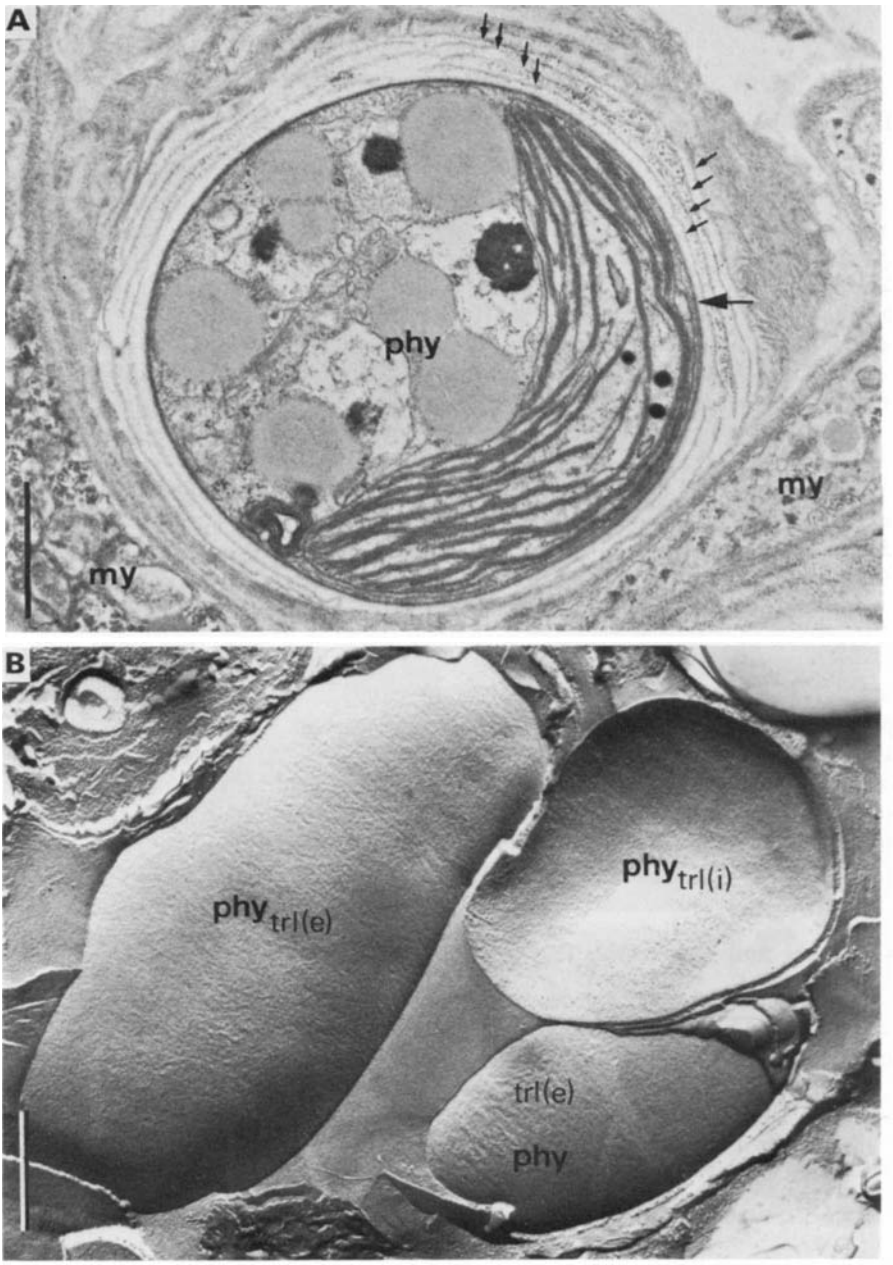


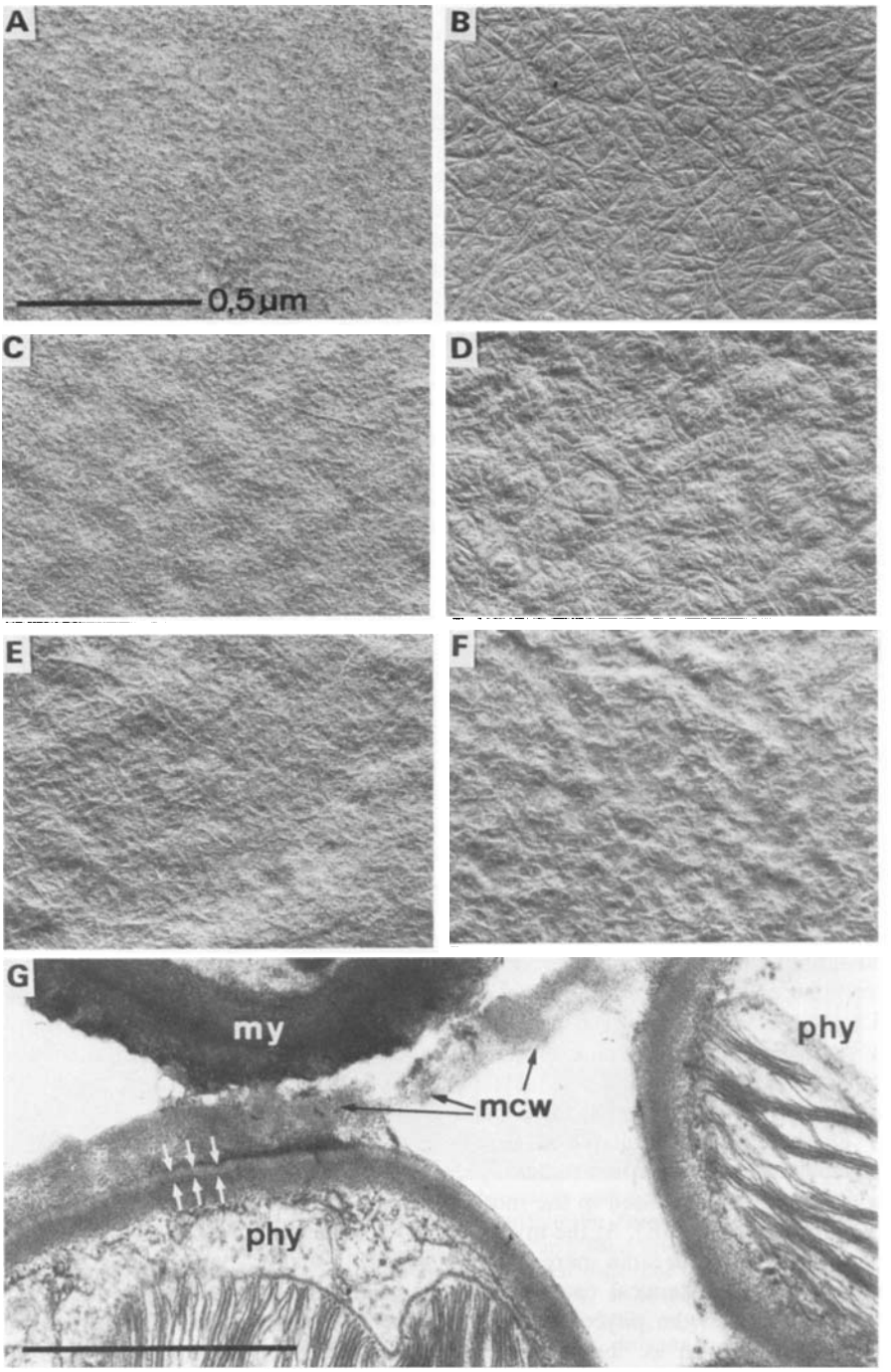
FIG. 6. Peculiarities of the cell wall of *Coccomyxa* phycobionts with a trilaminar, sporopollenin-containing outermost cell wall layer. A, Ultrathin cross-section of the *Coccomyxa* phycobiont (phy) of *Icmadophila ericetorum* with contacting mycobiont hypha (my). Small arrows point on a pile of persistant, non-degradable trilaminar layers of former mother cell walls. The large arrow points on the corresponding trilaminar wall layer of the functional cell wall. × 18 150. B, Freeze-fracture preparation of a group of *Coccomyxa* phycobiont cells in the thallus of *Peltigera venosa*. The fracture plane follows either the external (e) or internal (i) face of the very rigid, shell-like trilaminar outermost wall layer (trl) which contains the persistent biopolymer sporopollenin in a central part, but protein-like particles embedded in an amorphous matrix on the external and internal faces. × 16 000.

stage of development when the phycobiont cells are still enclosed within the mother cell wall (Fig. 4A; Tschermak 1941, Greenhalgh & Anglesea 1979, Honegger 1982*b*). This behaviour of the mycobiont was presumed to play a yet unknown rôle in the initial establishment of the symbiotic relationship, eventually in the transfer of metabolites between the symbionts, and later on in the distribution of the phycobiont cells within the growing edge of the thallus (Greenhalgh & Anglesea 1979). Moreover, the morphological observations on the mycobiont–phycobiont contact site may lead to the supposition that growing mycobiont hyphae must be able to recognize compositional and/or structural differences between young, functional phycobiont cell walls in which intraparietal haustoria are to be formed, and mother cell walls which are to be penetrated in order to contact the autospores.

Certain structural and probably also compositional changes were observed in replicas of the cell walls of the *Trebouxia* phycobionts of *Cladonia macrophylla* (Figs 7A–F) and in ultrathin sections of the trebouxioid phycobiont of *Parmelia tiliacea* (Fig. 7G; Honegger 1982*b*). In addition to these age-dependent structural alterations of the cell wall, compositional differences between the cell wall surface of cultured and symbiotic cells were detected in the trebouxioid phycobiont of *Xanthoria* species by cytochemical and immunological methods (Bubrick & Galun 1980*a*, *b*, Bubrick *et al.* 1981, 1982) and with fluorescence microscopy of the binding pattern of commercially available, FITC-conjugated lectins in trebouxioid and other phycobionts of various lichens (Marx & Peveling 1983). The question is now whether these compositional changes are correlated with structural alterations of the cell wall surface of the phycobiont.

In freeze-fracture preparations (for methods see Honegger & Brunner 1981) of thalli of *Cladonia macrophylla* very interesting cell wall surface layers were observed in the myco- and phycobiont which differ considerably from the cultured state (Figs 8A–G). The mycobiont hyphae of the medullary and algal layer of the thalli reveal a thin outermost wall layer with an irregularly tessellated pattern (Figs 8B, C), whereas mycobionts grown in liquid culture have a warty surface layer (Fig. 8A). The surface layer of symbiotic mycobiont hyphae in *Cladonia macrophylla* and other lecanoralean species has a certain similarity, but is structurally not identical with the rodlet layer observed in the three peltigeralean species so far investigated (see above; Fig. 5D). No distinct rodlets, but a mosaic of irregular ridges were detected each of which appears both in size and shape like a bundle of rodlets covered by a thin film of amorphous material. Surprisingly, a structurally identical outermost wall layer was found on the wall surface of phycobiont cells (Figs 8C, F). Confluence of the surface layers of myco- and phycobiont was observed at the contact sites (Fig. 8C).

The irregularly tessellated surface layer seems to be a characteristic of mature phycobiont cells. A distinct rodlet layer was observed on the surface of autospores which were still enclosed in the mother cell wall but already contacted by mycobiont hyphae (Fig. 8E). At the mycobiont–phycobiont contact site the rodlet layer of the autospore became increasingly covered by a thin, homogenous film of a material whose chemical composition and origin are unknown (Fig. 8E). With this coating film the phycobiont cell wall surface attained the same irregularly tessellated pattern as observed on the wall surface of the mycobiont. At the onset of mother cell wall degradation after autospore formation the irregularly



tessellated surface layer of the phycobiont disappears and the burled texture of the mother cell wall becomes obvious (Fig. 8G; compare with 7C, E).

Surface layers with irregularly tessellated pattern were so far detected on myco- and phycobiont cell walls of *Cladonia macrophylla* (Fig. 8), *Cladonia caespiticia*, *Hypogymnia physodes* and *Parmelia tiliacea* (all Lecanorales), and on the mycobiont cell walls of *Lobaria pulmonaria* (Peltigerales) and *Chaenotheca chrysocephala* (Caliciales; all unpublished).

The cytological observations on the cell wall surface layers in lichen symbionts raise a variety of questions. How are these surface layers chemically composed? Are the rodlet layer of autospores and the irregularly tessellated surface layer of mature phycobiont cells produced by the alga itself or are either one or both of them formed by the mycobiont and spread over the phycobiont cell wall surface? How far do these cytological findings correlate with the biochemical and immunological data of Bubrick *et al.* (1982), or does the surface layer with its irregularly tessellated pattern correspond to the compound which makes symbiotic phycobionts antigenically different from cultured ones? Does the surface layer play a rôle in recognition phenomena or in transfer processes between the symbionts? Is the disappearance of the surface layer with an irregularly tessellated pattern at the change from functional to mother cell wall the starting shot for neighbouring mycobiont hyphae to penetrate? Are such peculiar surface layers formed in resynthesized lichens as well, and at which moment, under which conditions? And

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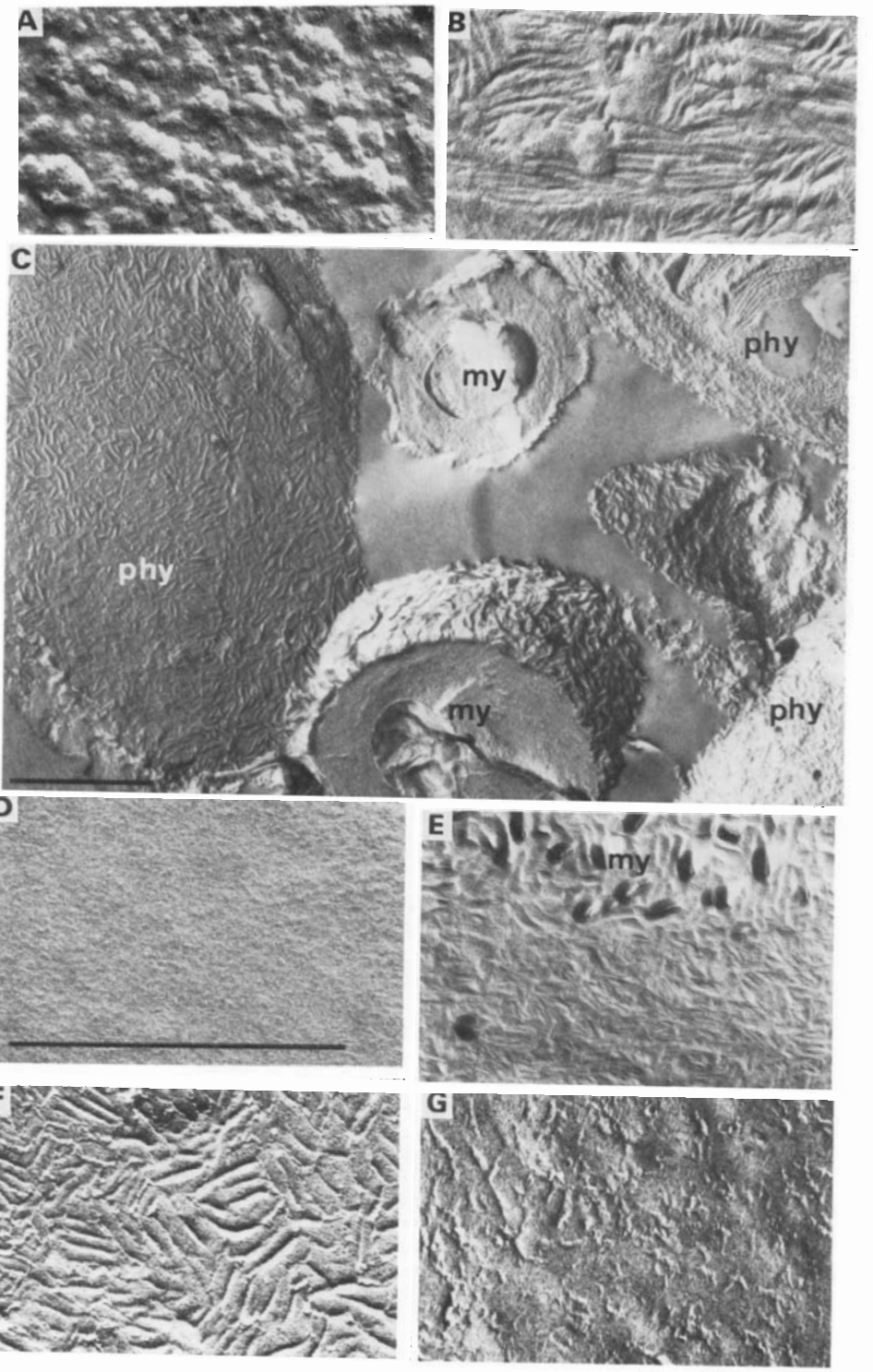
FIG. 7. TEM of replicas of isolated, purified cell walls of different developmental stages of the cultured *Trebouxia* phycobiont of *Cladonia macrophylla*. A,C,E, outer wall surface; B,D,F, inner wall surface. A–B, Cell wall of a mature phycobiont with smooth outer surface revealing protein-like particles embedded in an amorphous matrix and fibrous, probably cellulosic elements embedded in an amorphous matrix on the inner surface. C–D, Mother cell wall during or shortly after autospore formation; a burled texture is seen in the whole cell wall. E–F, Outer and inner surface of a mother cell wall at a later stage of degradation. The burled texture of the wall is more obvious than in C and D. The amorphous matrix of the outer surface layer was dissolved. A–F, ×48 000. G, TEM of an ultrathin section of the trebouxioid phycobiont of *Parmelia tiliacea*. Part of two autospores (phy) surrounded by part of the disintegrating mother cell wall (mcw) which reveals the same burled texture as observed in replicas of the phycobiont of *Cladonia macrophylla* (C–F). An electrontransparent outer wall layer (arrows) which corresponds to the smooth surface layer (A), and a more prominent, rather electrondense inner layer containing the fibrillar material can be distinguished in the young phycobiont cells. ×36 000.

FIG. 8. TEM of freeze-fracture preparations of the cell wall surface of the cultured and symbiotic myco- and phycobiont in *Cladonia macrophylla*. A, Cell wall surface layer with warty structure of the isolated mycobiont grown in liquid culture. B, Cell wall surface layer with irregularly tessellated pattern in the symbiotic mycobiont. A, B, ×48 000. C, Mycobiont (my)–phycobiont (phy) interface in the lichen thallus. The fracture plane follows from left to right the wall surface of a phycobiont cell (phy), then two broken mycobiont (my) hyphae the lower of which is contacting the phycobiont cell, then a broken phycobiont (phy) cell in the upper and the wall surface of phycobiont cell in the lower right. The irregularly tessellated surface layers of myco- and phycobiont cell walls are continuous at the contact site. ×20 000. D, Smooth cell wall surface with protein-like particles in the cultured *Trebouxia* phycobiont. E, Cell wall surface layer with rodlet pattern of a *Trebouxia* autospore which is still surrounded by the mother cell wall, but is contacted by a mycobiont hypha. The fungal hypha broke off, but at the contact site (my) the algal surface becomes increasingly covered by a thin film of amorphous material and attains an irregularly tessellated pattern. F, Cell wall surface layer of a mature phycobiont cell with irregularly tessellated pattern. G, Surface of a mother cell wall. The surface layer with irregularly tessellated pattern almost disappeared. The burled texture of the underlying, disintegrating mother cell wall is obvious (compare with 7C); D–G, ×48 000.



finally: are such features a peculiarity of some lichen symbioses or do they occur in other fungal-plant symbioses as well?

The answers to some of these questions are doubtless a long way off. However, the present study illustrates that lichens are especially suited for the investigation of a symbiotic relationship since the mycobiont–phycobiont interface is very easily accessible.

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